

NOTES ON THE LIFE CYCLE AND
MYRMECOPHILOUS ADAPTATIONS OF
CREMASTOCHEILUS ARMATUS
(COLEOPTERA: SCARABAEIDAE)

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INTRODUCTION

Adult cetonine scarabs of the genus *Cremastocheilus* are known for their association with ant colonies (Wheeler, 1908). The genus consists of approximately 40 species and has been recorded only in North America north of the Isthmus of Tehuantepec (Howden, 1971). Twenty-three species have been collected with 11 different genera of ants, yet their true relationship with the host ants remains unknown. Cazier and Statham (1962) and Cazier and Mortenson (1965) have summarized current knowledge of the genus based largely on their own studies of adult bionomics of several species from Arizona. The only information, however, on the development of the immature stages of this genus is a few scattered notes that the larvae of some species do occur in ant nests (Mann, 1911; Wheeler, 1908a; Windsor, 1964; and Ritcher, 1966).

This is the first account of the life history and development of *C. armatus* Walker, a western species (Fig. 1) occurring with different species of *Formica* ants from British Columbia to California and Nevada (Potts, 1945). The major host ant, *F. obscuripes* Forel, is one of the most common mound building ants in western North America. A very pugnacious and aggressive ant, *obscuripes* builds large mounds of soil and vegetation containing 50,000 or more individuals (King and Walters, 1950). How *armatus* survives from egg to adult within these nests was the object of field and laboratory studies.

METHODS

The following account is a synthesis of results obtained in western and central Oregon from 1957 to 1961 and eastern and western Washington from 1970 to 1975. All four study areas were charac-

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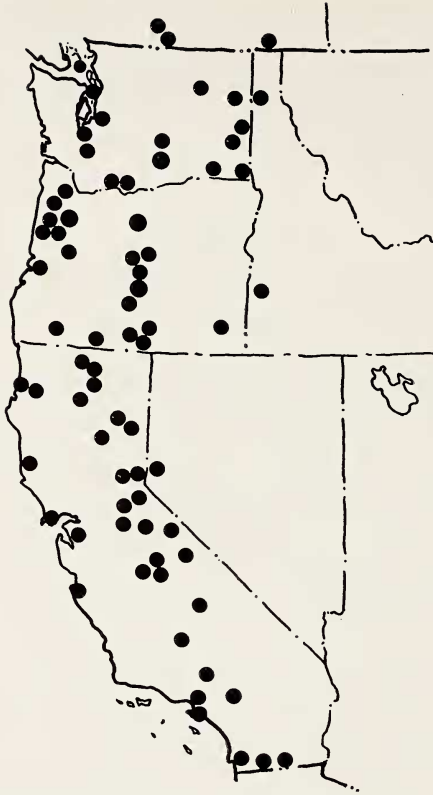


Figure 1. Distribution of *Cremastocheilus armatus* based on field collections and museum specimens.

terized by regions of high host ant density and the presence of a large population of *armatus* adults and immatures. Nest material was sorted, beetles were counted, and observations made on interactions with ants. All nest material was replaced to minimize the adverse impact of the sampling technique. The sex of the adult was identified in the field and later verified under a dissecting microscope. The sex was determined by evident geometrical differences of the last ventrite and the pygidium.

Adults and larvae were kept in the laboratory for many months with and without host ants. Larvae were most successfully reared in containers filled with original ant nest material. Adults were kept in closed containers at below room temperatures during the winter and were fed ant larvae the following spring.

LIFE HISTORY

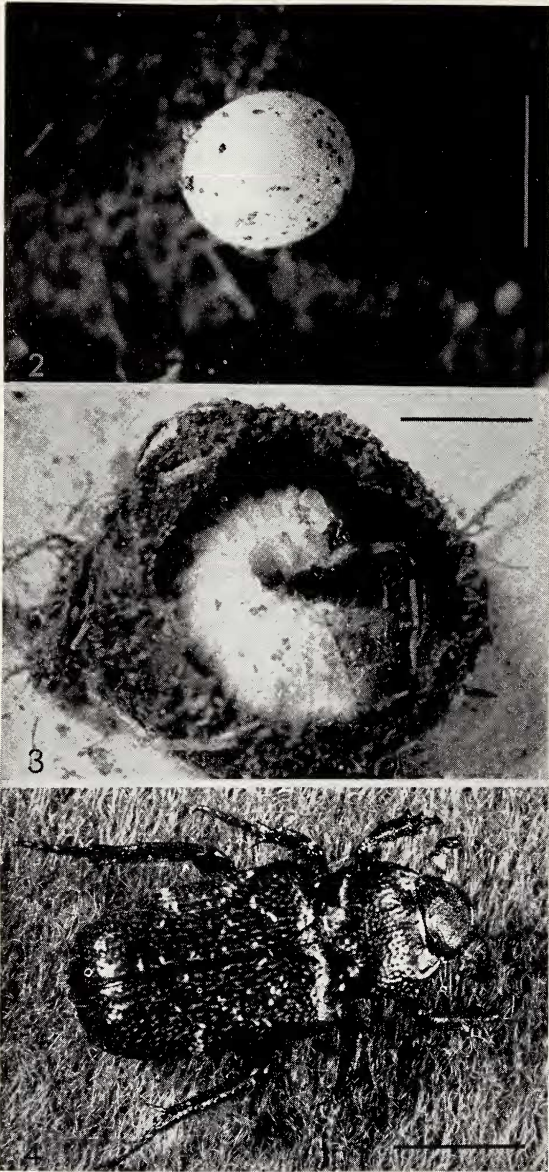
During the month of May, females laid eggs scattered throughout the outer soil edges of the ant nest. Here rich deposits of vegetative debris had accumulated and ant activity was low. Under laboratory conditions females laid a total of 3 to 12 eggs each. The broadly oval white eggs (Fig. 2) hatched after two weeks. First larval instars were collected until the middle of June. Second instars were found from June until the middle of July, and third instars were collected from the middle of June to the middle of August. The pupal stage lasted two more weeks, indicating that under field conditions development from egg to adult occurred in less than 4 months.

Most ant nests contained fewer than 30 larvae, although several nests contained well over 200. Second and third instars were gregarious, feeding within the vegetative debris just below the soil surface. Late third instars were darkened posteriorly due to the large number of fecal pellets retained in the abdomen. When uncovered, the larvae were quickly seized and bitten by many ants. They escaped the ants by rapidly burrowing down through the nest material. Late third instars left the outer soil edges and moved inward towards the center of the thatch mound to pupate. This took place during the hotter days of July when the ants were not very active in the upper mound area.

In the dry twig area above the ants' brood chamber larvae constructed elliptical earthen cases within which they pupated (Fig. 3). Easily damaged when newly formed, several of these pupal cases soon dried and hardened together into a protective clump. Adults eclosed during the late summer days and a few could be found on the surface of ant mounds at this time (Fig. 4).

As colder weather approached, the beetles moved deeper within the nest, often ending up a meter or more below the soil surface. Here the adults overwintered surrounded by dormant ants (Fig. 5). Periodic collections of overwintering adults revealed that within a few minutes at room temperature the beetles became active, even if temperatures outside the nest were below 10° C. Females often laid several eggs within a few days at room temperature but none of the eggs laid during the winter period hatched.

The following spring the adults moved back up to the outer areas in the mound. Most of the adults were collected within 3 centimeters of the nest surface at this time. Flight was so rapid at temperatures above 24° C. that mark and recapture methods were unsuccessful in determining the flight range. During this same period adult beetles



Figures 2-4. Developmental stages of *Cremastocheilus armatus* (2) Egg. (3) Late third larval instar inside earthen case. (4) Adult. (Scale: fig. 2 = 2mm; figs. 3 and 4 = 4mm).

readily fed on ant larvae and pupae. As many as 85 pairs (male and female) of adult *C. armatus* were collected in the outer nest galleries. Although they were not *in copula*, the females later laid fertile eggs. No mating was ever observed in the nest or in the laboratory. Data from museum collections indicate a peak of flight activity during April and May, the time during which mating may occur. Gravid females normally laid their eggs below the surface at the periphery of the nest.

Host records for *armatus* are probably incomplete (Table 1). *F. obscuripes* is the most common host but dispersal flights may introduce these beetles into a wide variety of ant nests. In western Oregon adults were collected from *Formica fusca* mounds, although immature stages were never found there. Larvae have been collected and reared from rich garden soil in western Oregon (Ritcher, 1966) indicating that under certain circumstances the immature stages may not have an obligatory relationship with ants.

Table 1. Host records for *Cremastocheilus armatus*

Host	Locality	Collector	Life-Stage	Reference
<i>Formica obscuripes</i>	E. Wash.	Mann	adult/larvae	Mann (1911)
	W. Wash.	Alpert	adult/larvae	New Record
<i>Formica fusca</i>	W. Oregon	Ritcher	adult	New Record
<i>Formica subpolita camponoticeps</i>	British Columbia	Howden	adult	Cazier (1962)
<i>Formica integra tahoensis</i>	E. Oregon	Ritcher	adult/larvae	Ritcher (1966)
<i>Formica integroides subnitens</i>	British Columbia	Ayre	adult	Cazier (1962)

LARVAL DEFENSE

To examine escape behavior, larvae were removed from the ant nests and placed in a series of containers with one to several ants. The normal feeding position of the larva is a C-shaped curve with the head and anal area closing off the ventral region from attack. The

ants readily attempted to bite the larvae but were unable to grasp a larva firmly with their mandibles from a dorsal approach because the dorsal surface was too convex. If however an ant came into contact with the head or ventral region there was a very rapid strike response from the larva. The larva struck at the ant with its mandibles as it coiled more tightly into the C-shape. A dark fluid was released from between the larval mandibles at the time of the strike. As the larva wriggled to escape, several wet fecal pellets were expelled which had a deterrent effect on aggressive ants. There was also a strong, unpleasant odor associated with the mandibular and anal secretions.

The above reaction was repeated until the mandibles made contact with and crushed the body of the ant. When this happened the ant immediately released its grasp of the larva and within a few seconds it collapsed. Movement was usually limited to tremors of the appendages until death occurred. Occasionally a beetle larva was fatally injured by attack from too many ants. The mandibular strike was most effective when a minor worker ant was attacked by a third instar larva.

ADULT DEFENSE

When first attacked, the beetle assumed a characteristic death feigning posture with all its legs out and slightly up at the sides. In the laboratory this position was seldom held for less than 5 minutes and showed little habituation. The ants grasped the beetles by their legs and pronotal projections and dragged them randomly about, eventually releasing their hold. Host ants regularly attacked beetles on the mound surface but as the beetles burrowed down into the thatch, most of the ants were removed. Beetles were able to penetrate the mound surface in less than one minute. In addition the beetle's heavily sclerotized integument, retractible antennae, and concealed mouth parts also represent adaptations for survival in ant nests.

If the beetle was violently disturbed or turned over by the ants, a droplet of viscous fluid was released from the anal opening. This fluid had an offensive odor and was effective in repelling the ants. When an ant came into physical contact with this fluid, it became agitated and spent considerable time grooming. Defensive secretions have been documented for other myrmecophiles (Hölldobler, 1970; Blum et. al., 1971) and their discovery in other species of *Cremastocheilus* is expected.

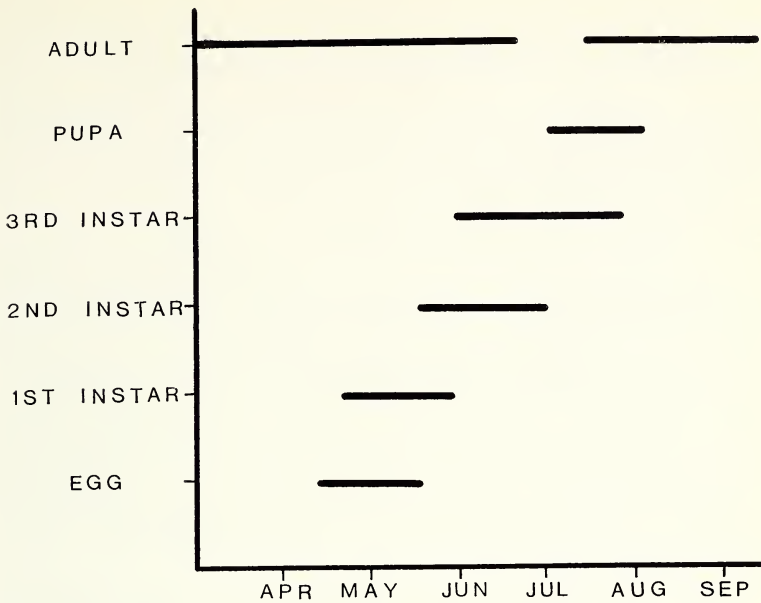


Figure 5. Seasonal distribution of the developmental stages of *Cremastocheilus armatus* collected from *Formica obscuripes* ant mounds.

PREDATION

During the spring adult beetles were predaceous on both ant larvae and pupae. In the field beetles were found feeding on larvae near the brood chamber while at the same time beetles in the outer galleries were motionless, suggesting that individuals moved into the center of the nest to feed and returned to the periphery when satiated. In the laboratory predation increased when beetles were deprived of food for over one month and when containers were darkened. It was not unusual for several beetles to feed on one ant larva at the same time.

Unlike other scarabs, *Cremastocheilus* has an unusual cupshaped mentum which prevents ants from contacting the beetle's mouth parts. When feeding, a beetle lowered its mentum and pierced an ant larva with its sharp maxillae. The mandibles are greatly reduced and aid in the transport of fluid. Feeding lasted from 10 to 30 minutes as the beetle slowly pumped the ant larva dry. Beetles were not disrupted from feeding even when covered with attacking ants.

C. armatus has fed on the larvae and pupae of the carpenter ant, *Camponotus* sp. in the laboratory (J. T. Doyen, pers. comm.). The larvae and pupae of other species of non-host *Formica* sp. have also been consumed. This lack of specificity may account for those species of ants that serve as alternate hosts, and for the wide distribution of *armatus*.

TRICHOMES

Hölldobler (1971) has shown that myrmecophiles have the ability to communicate in the same chemical language as their hosts. Trichomes are tufts of hairs that serve to increase the ability of well-integrated ant guests to communicate chemically. They are located on the ventral surface of highly modified anterior and posterior pronotal projections of *Cremastocheilus* adults. The pronotal projections have been cited as being modified to fit the mandibles of ants and to contain glands which emit a stimulating and attracting odor (Wheeler, 1908). It has been proposed that these beetles are brought into the nest and held captive by the ants because of this odor (Cazier and Mortenson, 1965).

The role of trichomes in the relationship of *C. armatus* to its host, *F. obscuripes*, is unknown. The ants do not appear to be specifically attracted to trichome areas nor are the beetles held captive by the ants. *C. armatus* is usually found unattended by ants within the nest, and is attacked by ants when on the nest surface.

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